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Wildlife and Fisheries Habitat Management Notes

Habitat Relationships of Sitka Black-Tailed Deer

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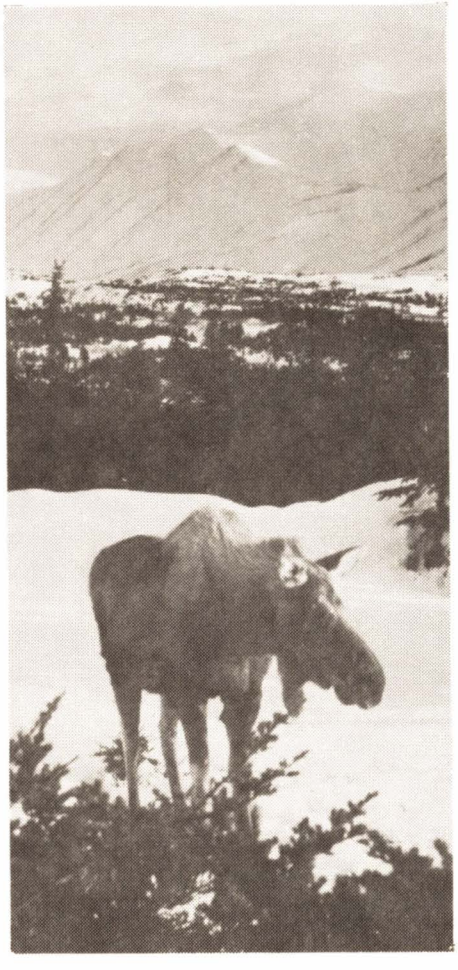

Abstract

Sitka black-tailed deer are endemic to southeastern Alaska where old growth, western hemlock-Sitka spruce forest is an important feature of their habitat. The conversion of uneven-aged, old-growth forests to even-aged, second-growth forests has generated concerns about the future carrying capacity of the habitat for deer, especially where snow accumulation is common on winter ranges. In this report, the ecological bases of deer-habitat relationships are reviewed and synthesized into a framework for evaluating habitat quality. Nutritional relationships, especially those involving energy, are emphasized. Data from southeastern Alaska provide insight into fundamental cause-effect relations between deer and their forest habitat. Key relationships are those between forest canopy and its effect on understory production and snow interception, and those between the metabolic requirements of deer and the nutritional quality of available forage. Indications are that conversion of uneven-aged old-growth stands to even-aged stands generally will result in decreased carrying capacity of habitat for deer. Implications for forest management are addressed, and needs for future research are identified. The current theory is largely qualitative and lacks the ability to yield unambiguous, quantitative predictions. Qualitative predictions, however, are possible.

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Habitat Relationships of Sitka Black-Tailed Deer

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Credits

This report largely duplicates that of Hanley (1984. Relationships between Sitka black-tailed deer and their habitat. Gen. Tech. Rep. PNW-168. Portland, OR: U.S.D.A., Forest Service, Pacific Northwest Forest and Range Experiment Station. 21 p.). It differs from that report primarily in its section on Management Implications. All figures, except figure 7, are directly from Hanley (1984). Figures 6, 7, and 10 were from earlier published reports and are used with the authors' permission.

Fig. 1. Present distribution of Sitka black-tailed deer.

Introduction

Sitka black-tailed deer are endemic to the north Pacific coast from about 53° to 58° N latitude (Queen Charlotte Sound, British Columbia, to Icy Strait, Alaska), occupying all of the Alexander Archipelago and a narrow strip of adjacent mainland (Fig. 1). Transplants have established populations on the Queen Charlotte Islands, the Yakutat area, Prince William Sound, and Afognak and Kodiak Islands (Wallmo 1981).

Deer harvests are small (about 3-14,000 annually, Johnson and Wood 1979) compared to those in most western states, but they confer status to deer as a major game species in Alaska. Deer densities on winter ranges have been estimated as high as 25-75 deer km^{-2} (Barrett 1979; J. W. Schoen and O. C. Wallmo, unpublished data). Experienced observers believe that the populations are subject to large fluctuations. Generally, declines are related to attrition from starvation during winters with deep snow, and increases to successive open winters in which snow does not restrict their range excessively (Klein and Olson 1960, Merriam 1968, Olson 1979, Reynolds 1979, Smith 1979).

Sitka black-tailed deer inhabit the northwestern-most extension of the range of mule and black-tailed deer (Wallmo 1981). This is a region of coastal coniferous rainforest. The maritime influence moderates temperatures, but levels of precipitation are high year-round. Historically, fire frequency has been low, and windthrow has been the major source of disturbance to the forests (Harris and Farr 1974). Consequently, the region is characterized by uneven-aged, old-growth forest, with alpine vegetation at higher elevations (commonly down to 400 m). Although temperatures are mild, compared to continental climates, Sitka black-tailed deer are subject to much greater depths of snow for a longer period of time than are their more southern counterparts, Columbian black-tailed deer.

The ability of deer to survive the inclemency of winter is influenced by the nutritional condition in which they enter the winter, the duration of severe forage restriction, and the amount of forage available to them at the end of the winter. Although subalpine habitat constitutes an important part of the summer range in Alaska, the winter range is restricted to forest habitats. As snow accumulates, deer populations become concentrated on winter range. Forest management practices which alter the quality of winter range for deer will have greater consequences than might be inferred from considering only the acreages affected. This is especially true if the practice affects the higher quality patches of winter range.

Because of the increase in logging in southeastern Alaska during the past 30 years, it is clear that in the future an increasing percentage of the deer habitat will be in some stage of post-logging succession. The effects of timber harvesting and stand improvement practices on the quality of habitat for deer are a major concern in southeastern Alaska.

The purpose of this report is to review the ecological bases for deer-habitat relationships, to summarize the current state of knowledge about relationships between Sitka black-tailed deer and forests, to address the implications for forest management, and to identify needs for future research.

Ecological Bases of Deer-Habitat Relationships

Nutrition and Diet

Energy. An understanding of deer-habitat relationships requires an understanding of seasonal changes in the availability and quality of food and the physiological requirements of deer. During summer, both the quantity and quality of forage are relatively high, and deer gain weight (Table 1). During winter, however, both the quantity and quality of forage are low, and deer lose weight. Even in the absence of snow, deer lose weight during winter and must catabolize body reserves, principally fat and muscle tissue (Bandy et al. 1970). The amount and duration of snow accumulation on the ground, however, is of critical importance to the winter survival of deer. As snow buries forage, diet quality decreases, as does dry matter intake, and daily energy intake decreases (Table 1). At the same time, energy costs of locomotion increase as deer sink deeper into snow (Fig. 2).

Energy costs of reproduction are also substantial. Sexual differences in reproductive costs are apparent in differences in annual fat cycles (Fig. 3). Although both male and female deer gain weight over summer and lose it over winter, the seasonal gains and losses occur earlier for males than for females. The pattern of weight gain in males follows naturally from the seasonal changes in the quality and availability of forage; but because of substantial weight losses during the rut in late fall, males generally enter the winter in poorer condition (lower fat and nutrient reserves) than do females (Fowler et al. 1967, Nordan et al. 1968, Anderson et al. 1972). Adult males are especially active during the rut and spend little time foraging (Nordan et al. 1968, Geist 1981). For females, late summer and fall is the time when weight gains are greatest (Anderson et al. 1972, Mitchell et al. 1976). Forage quality and quantity are still relatively high, reproductive demands are relaxed, and energy and nutrient intake generally exceed maintenance requirements (Short 1975). High costs of gestation and lactation (Fig. 4) usually preclude weight gains by reproductive females during spring and summer although forage quality and quantity are at their peaks.

Reproductive costs for the pregnant female are insignificant during the most severe conditions of winter. As gestation progresses through spring, however, the availability of nutritious forage is critical for successful reproduction.

Table 1. Estimated daily energy requirement for maintenance and daily energy intake for an adult doe black-tailed deer.

	SUMMER	WINTER w/o snow	WINTER w/snow
Body Wt.[1] (kg)	45	50	50
AMR[2] (kcal d^{-1})	2,432	2,632	2,632
Dry Matter Intake[3] (g $kg^{-0.75}$ d^{-1})	80	59	48
Dry Matter Digestibility[4] (%)	70	55	35
Energy Intake[5] (kcal d^{-1})	3,722	2,334	1,208
Net Energy Gain (+) or Loss (−) (kcal d^{-1})	+1,290	−298	−1,424

[1] Body weights are for an adult (2-yr-old) doe in early summer and early winter (source: Bandy et al. 1970).

[2] AMR=Activity Metabolic Rate=**c** (BMR), where **c** is a constant that varies with seasonal activity levels, and BMR is Basal Metabolic Rate or approximately 70 times body weight (kg) to the 0.75 power. BMR also varies seasonally. (source: Moen 1973, Wallmo et al. 1977).

[3] Ovendry weight of forage consumed per $kg^{0.75}$ body weight per day (source: Bandy et al. 1970, Alldredge et al. 1974). Intake is lower during winter with or without snow.

[4] Source: Wallmo et al. 1977, Rochelle 1980, Short 1981.

[5] Energy Intake=**GE de me (DMI),** where GE is the gross energy content (4.5 kcal g^{-1}), **de** is dry matter digestibility, **me** is the metabolizable energy coefficient (0.85), and **DMI** is dry matter intake.

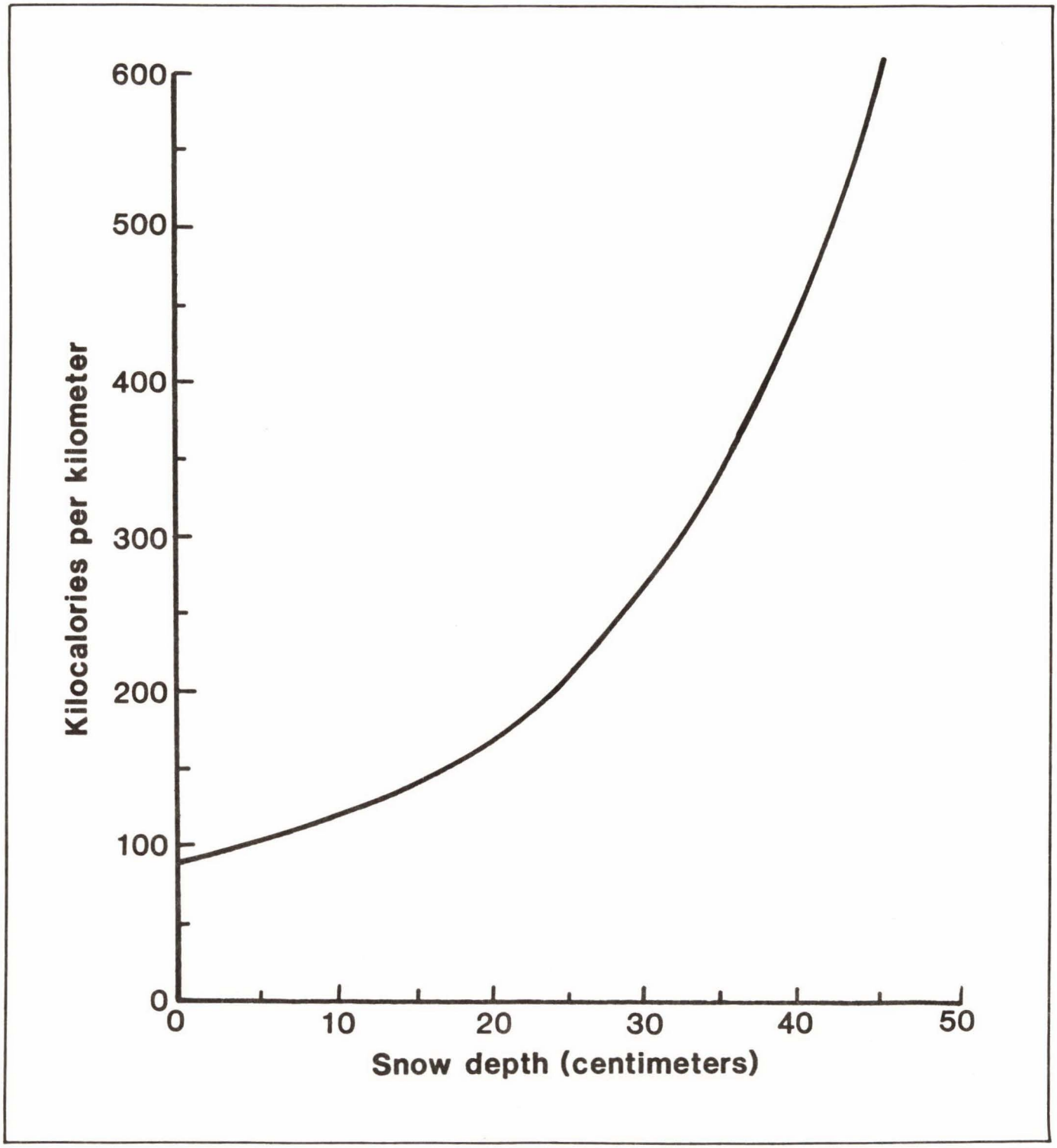


Fig. 2. Energy costs of locomotion through snow for a 40-kg deer (source: Mattfeld 1974).

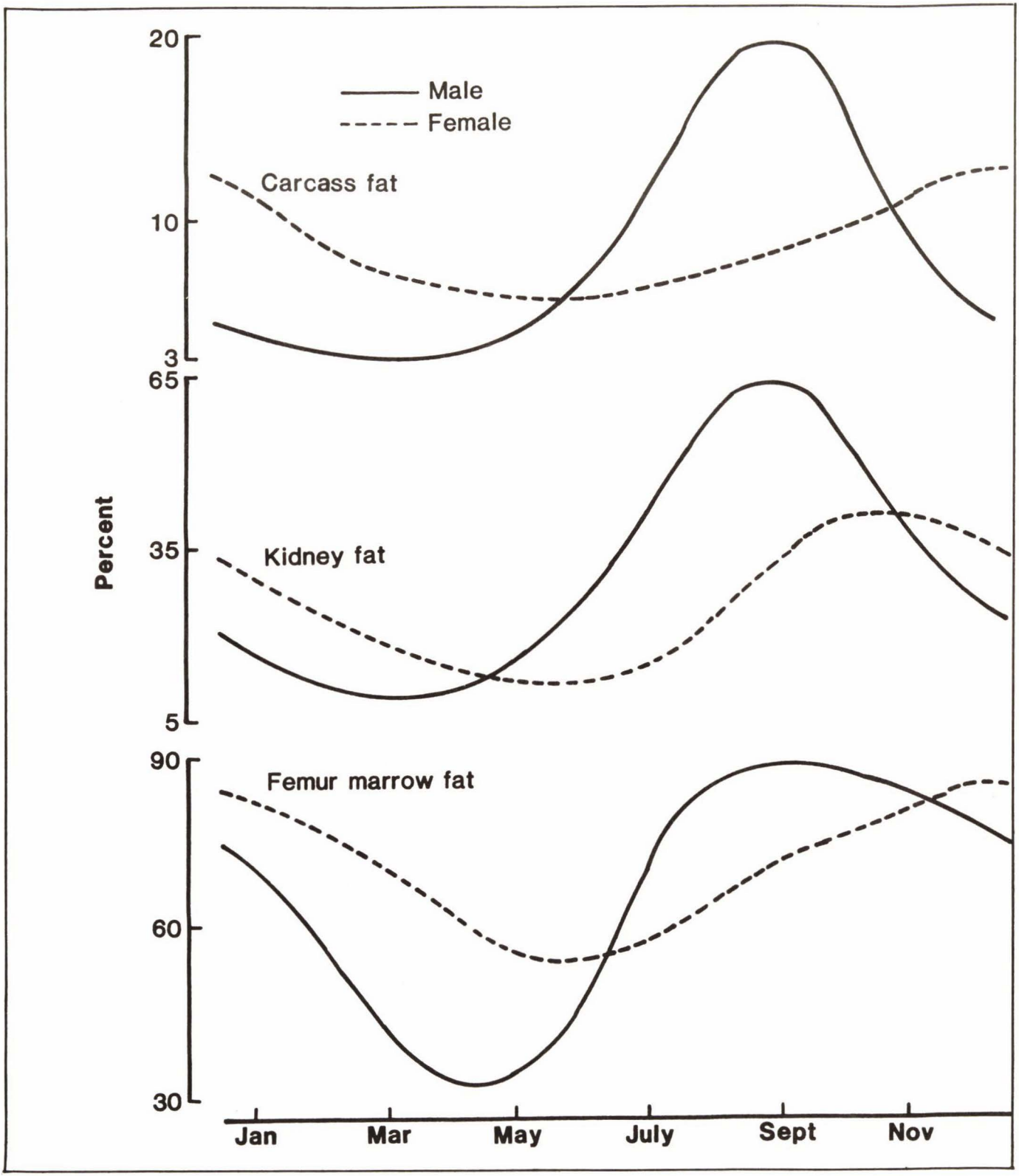


Fig. 3 Annual cycle of fat storage and depletion in mule deer (after Anderson et al. 1972).

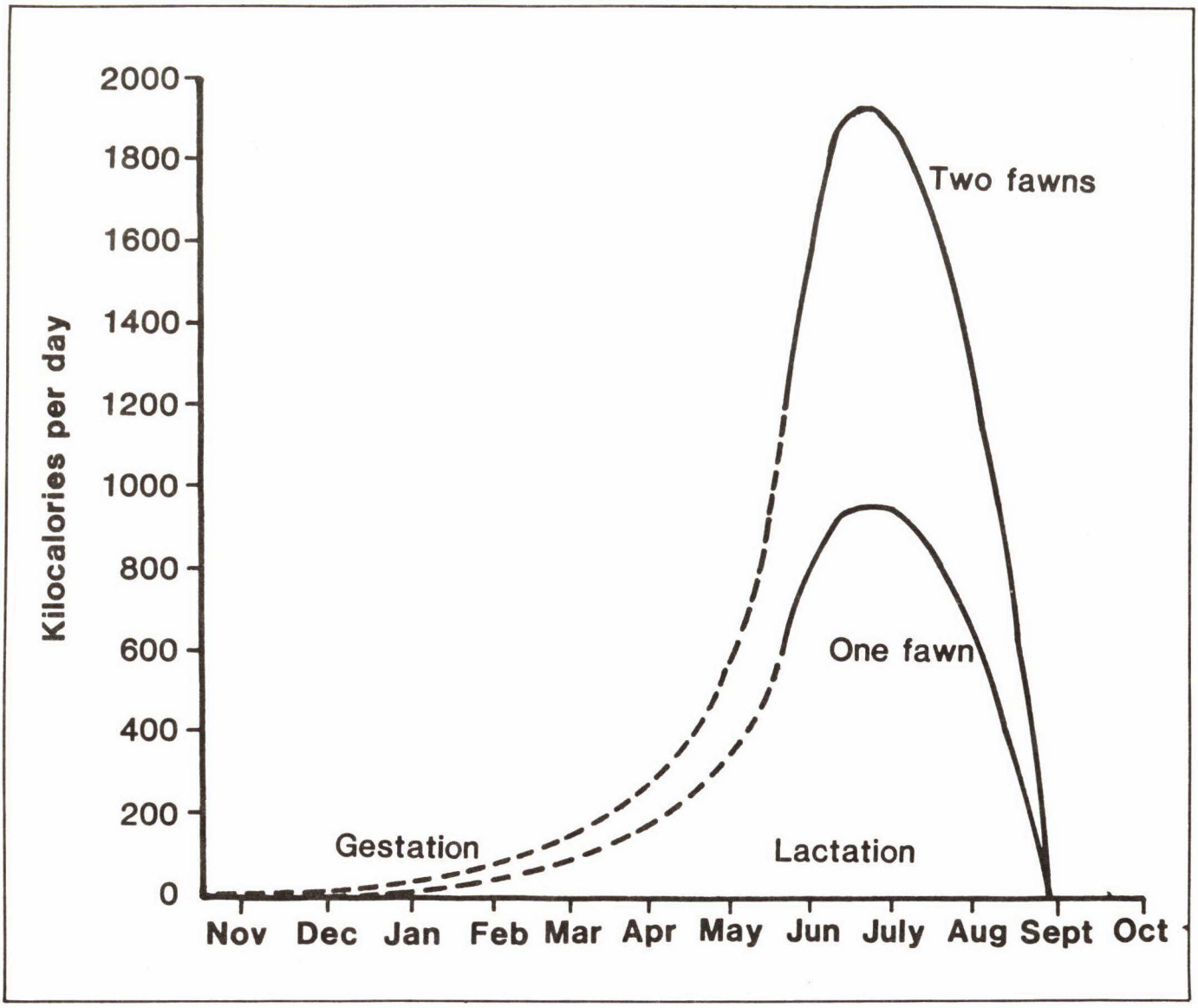


Fig. 4. Energy requirements (kcal d^{-1}) for gestation and lactation for a doe with one or two fawns (source: Moen 1973, Robbins and Moen 1975).

Plant Nutrients and Secondary Compounds. Although specific mineral elements are known to be required by deer, deer-habitat relationships are understood best in terms of energy and nitrogen metabolism (Moen 1973). Energy is needed to "fuel" the deer, while nitrogen is needed for protein synthesis to build body tissue. The cell-soluble fraction of forage contains the majority of nitrogen and mineral nutrients as well as readily digestible energy sources of sugars, starches, and fats, whereas the cell-wall fraction is chiefly an energy source only (Van Soest 1967). For black-tailed deer, with a feeding strategy that emphasizes the cell-soluble fraction (Hanley 1980), nitrogen, mineral nutrients, and energy sources are closely related dietary constituents. Diets which are high in digestible energy also tend to be high in nitrogen and essential minerals as well. The rumen microflora synthesizes B-complex vitamins, and vitamin deficiencies for deer are apparently very rare (Short 1981).

Plants also contain compounds that are deleterious to deer. Many such compounds have been considered as secondary by-products of plant metabolism, but more recently they have been viewed as "anti-herbivore defense mechanisms" (reviews by Feeny 1976, Levin 1976, Rhoades and Cates 1976). Plant secondary compounds are basically of two kinds: (1) toxins and (2) digestibility-reducing substances. While most plants employ both kinds, one or the other usually predominates in certain types of tissue. Toxins tend to be very specific and dose-dependent, so their effects can be reduced or avoided by an herbivore by consuming a mixed-species diet. Digestibility-reducing compounds are more general and not dose-dependent, so their effects may be more difficult for an herbivore to overcome. Digestibility-reducing compounds commonly interfere directly with nitrogen availability by forming indigestible complexes with proteins and enzymes (Feeny 1975, Mould and Robbins 1981), thus reducing nitrogen availability to the herbivore below that indicated by nitrogen content of the forage. The content of secondary compounds varies among individuals within species and among species, and deer may select among them accordingly (Radwan 1972, Radwan and Crouch 1974, Dimock et al. 1976). When deer are selective for this or other reasons, the real forage availability may be less than the current annual growth of the species. While maximizing energy intake may be a goal in determining the optimal diet, it can be accomplished only within the constraints imposed by minimum requirements for nutrients and maximum tolerances of secondary compounds. Since the chemical composition of plants differs greatly among species, forage variety and a mixed diet are very important to deer (Freeland and Janzen 1974, Westoby 1974, Milchunas et al. 1978, Carpenter et al. 1979, Mould and Robbins 1981).

Table 2. Plant species reported to have been eaten by Sitka black-tailed deer.

Species	Source
Forbs	
Aruncus sylvester	Pierce 1981
Caltha biflora	Klein 1963
Caltha palustris	Pierce 1981
Coptis aspleniifolia	Merriam 1970, Reynolds 1979
Coptis trifolia	Merriam 1970
Epilobium angustifolium	Merriam 1965 and 1968, Pierce 198l
Fauria crista-galli	Klein 1963, Merriam 1971a, Pierce 1981
Heracleum lanatum	Merriam 1964
Listera spp.	Klein 1965
Lysichiton americanum	Klein 1963, Merriam 1971a, Pierce 1981
Maianthemum dilatatum	Merriam 1965 and 1967, Reynolds 1979
Potentilla spp.	Pierce 1981
Streptopus spp.	Merriam 1965
Tiarella trifoliata	Merriam 1965 and 1967, Reynolds 1979
Vicia gigantea	Pierce 1981
Viratrum viride	Merriam 1965
Ferns	
Athyrium filix-femina	Smith 1979
Blechnum spicant	Pierce 1981
Dryopteris spp.	Merriam 1965 and 1967
Polystichum munitum	Klein 1963
Pteridium aquilinum	Pierce 1981
Thelypteris limbosperma	Pierce 1981
Graminoids	
Calamagrostis spp.	Merriam 1964
Carex spp.	Klein 1963
Deschampsia spp.	Merriam 1964
Elymus arenarius	Olson 1952
unspecified species	Merriam 1968, Pierce 1981
Half-shrubs	
Cornus canadensis	Merriam 1965, 1967, 1970, and 1971a, Reynolds 1979, Pierce 1981
Empetrum nigrum	Pierce 1981
Empetrum spp.	Merriam 1968
Loiseleuria procumbens	Pierce 1981
Oxycoccus microcarpus	Smith 1979
Rubus pedatus	Merriam 1965, 1967, and

Species	Source
	1970, Reynolds 1979
Vaccinium uliginosum	Klein 1963
Shrubs	
Arctostaphylos uva-ursi	Merriam 1968
Betula spp.	Smith 1979
Cladothamnus pyrolaeflorus	Pierce 1981
Gaultheria shallon	*Pierce 1981*
Menziesia ferruginea	Klein 1957b, Pierce 1981
Oplopanax horridum	Klein 1963
Ribes spp.	Pierce 1981
Rosa nutkana	Merriam 1964
Rubus spectabilis	Merriam 1964
Rubus spp.	Pierce 1981
Salix spp.	Merriam 1968
Sambucus racemosa	Klein 1963, Merriam 1964, Pierce 1981
Vaccinium spp.	Olson 1952, Klein 1957a, 1957b, and 1963, Olson and Klein 1959, Merriam and Batchelor 1963, Merriam 1965, 1967, 1968, 1970, 1971a, and 1971b, Pierce 1981
Viburnum edule	*Smith 1979, Pierce 1981*
Trees	
Alnus spp.	Merriam 1968
Chamaecyparis nootkatensis	Pierce 1981
Picea sitchensis	Merriam 1968, Klein 1963
Pinus contorta	Pierce 1981
Thuja plicata	Pierce 1981
Tsuga heterophylla	Olson 1952, Klein 1963, Merriam 1965, Pierce 1981
Tsuga mertensiana	Klein 1957b
Lichens	
Unspecified species	Smith. 1979, Pierce 1981
Mosses and Liverworts	
Unspecified species	Pierce 1981
Algae	
Fucus spp.	Olson 1952

Diet Composition. A list of plant species known to have been eaten by Sitka black-tailed deer can be obtained by compiling the records in the literature (Table 2). Food selection by black-tailed deer has been reviewed recently by Crouch (1979), Taber and Hanley (1979), and Pierce (1981). Lists of forage species, however, provide little information about diet selection and the relative importance of diet constituents. Of greater value is an understanding of the characteristics of forages that are most valuable to deer (Hanley 1982a). The potential quality of forage can be judged on the basis of relative content of cell solubles and cell-wall materials (Table 3).

Although limited, data from southeastern Alaska (Table 4) indicate the forages are similar in chemical composition to those from western Washington (Hanley 1980) and Vancouver Island, B.C. (Rochelle 1980). During the growing season, actively growing plant tissue, especially shrub leaves and forbs, contains the greatest proportion of cell solubles and nitrogen and is the most valuable deer forage. Plants growing in subalpine and alpine habitats are especially nutritious during summer (Klein 1965). During winter evergreen shrubs and forbs (e.g., bunchberry, five-leaved bramble, fernleaf goldthread, lace flower, single delight) are the most valuable forage resources (Schoen and Wallmo 1979). Although deciduous shrubs and conifer foliage are eaten, the herb-layer forages, if available, comprise the major portion of the diet (Table 5). Where available, arboreal lichens (e.g., beard lichen) are readily eaten by deer. They constitute a potentially valuable energy source and may increase the digestibility of other forages (Rochelle 1980).

Snow accumulation affects availability of forage species differentially. The lower, evergreen, herb layer containing the higher quality forage is covered before the lower quality conifers and tall, deciduous shrubs (Harestad 1979). In general, the effect of snow on forage quality is disproportionately greater than its effect on forage quantity. In terms of the winter energy budget of deer, with the herb-layer, evergreen forages buried, energy deficits increase greatly despite the availability of an abundance of deciduous browse and conifers (Markgren 1971, Kucera 1976, Perzanowski 1978).

Table 3. Cell wall composition and estimated digestibility of some major classes of deer forage (after Short 1981)

Food	Cell Solubles	Cell Wall	Holocel-lulose	Lignin	Estimated digestibility	
	Percentage dry weight					
					A[1]	B[2]
Grasses						
immature	63	37	33	4	87	94
mature	15	85	70	15	56	20
Forbs						
immature	56	44	33	11	71	69
mature	25	75	57	18	53	27
Woody twigs						
immature	64	36	24	12	73	75
mature	38	62	39	23	52	40
Leaves						
green	69	31	18	13	73	71
fallen	51	49	23	26	50	45
Fleshy fruits	59	41	21	20	64	69
Mushrooms	61	39	37	2	93	95
Lichens *(Alectoria sarmentosa)*						73[3]

1. A is estimated true digestibility, from cell wall content and composition.
2. B is estimated true digestibility measured by the nylon-bag technique.
3. Annual mean, from Rochelle (1980) for *in-vitro* dry matter disappearance.

Table 4. Chemical composition of 11 winter forage species collected in January.

	Cell Solubles	Cellulose	Hemi-Cellulose	Lignin/ Cutin	Ash	Nitrogen
	Percentage Composition					
Pyrola secunda	78.3	15.1	3.0	3.0	0.6	3.14
Tiarella trifoliata	76.3	18.3	2.4	2.6	0.4	2.00
Rubus pedatus	67.3	17.3	11.0	3.8	0.6	1.94
Cornus canadensis	66.8	18.1	6.8	7.8	0.5	1.66
Coptis aspleniifolia	61.1	25.4	8.2	4.7	0.6	1.62
Rubus spectabilis	36.0	27.5	16.8	18.7	1.0	1.79
Tsuga heterophylla	54.8	24.3	5.5	14.8	0.6	1.50
Vaccinium spp.	37.9	29.8	13.1	17.4	1.8	1.46
Menziesia ferruginea	38.5	25.5	15.4	19.0	1.6	1.39
Usnea spp.	84.0	2.7	11.8	1.3	0.2	0.56
Liverwort	49.2	20.6	23.4	3.0	3.8	1.89

Source: Calculated from data in Schoen and Wallmo (1979:80)

Table 5. Plant species composition (percentage oven-dry weight) of rumen contents from 14 Sitka black-tailed deer. All deer were collected during virtually snow-free conditions at sea level, January-March 1981, Admiralty and eastern Chichagof Islands. (from D. E. Spalinger 1981, unpublished report on file at USFS Forestry Sciences Laboratory—Juneau). t = trace = less than 0.05.

	Rumen Composition (percentage oven-dry weight)				
Plant Species	January (n=4)	February (n=9)	March (n=1)	Mean (n=14)	Range
Forbs and Ferns					
Coptis aspleniifolia	12.9	4.8	18.6	8.1	0-18.6
Dryopteris dilatata	0	5.4	0.1	3.5	0-37.9
Lysichiton americanum	6.0	1.7	16.2	4.0	0-18.6
Tiarella trifoliata	0.4	2.8	0.4	1.9	0-11.5
Half-shrubs					
Cornus canadensis	37.5	35.5	16.1	34.7	13.6-54.1
Empetrum nigrum	0.1	0	0	t	0- 0.3
Phyllodoce aleutica	0	0	5.5	0.4	0- 5.5
Rubus pedatus	10.4	6.0	6.0	7.3	1.1-31.9
Vaccinium vitis-idaea	0.1	t	1.6	0.2	0- 1.6
Vaccinium spp.[1]	0.7	1.0	1.9	1.0	0- 2.9
Shrubs and Trees					
Chamaecyparis nootkatensis	0	15.7	0.6	10.1	0-46.8
Ledum palustre	4.8	0.9	11.3	2.8	0-18.9
Picea sitchensis	0	t	0	t	0- 0.1
Rubus spectabilis	7.5	0	0	2.1	0-17.0
Tsuga heterophylla	*1.0*	*9.8*	*3.5*	*6.8*	*0.4-25.8*
Vaccinium spp. stems	3.2	3.1	4.6	3.2	0- 9.9
Unidentified stems	3.8	6.8	10.6	6.2	
Lichens					
Usnea spp.	1.4	0.6	0.3	0.8	0- 3.0
Other lichens	0.2	3.3	0.3	2.2	0-14.1
Graminoids	t	0.1	0.3	0.1	0- 1.0
Algae					
Fucus furcatus	6.9	1.1	2.2	2.8	0-16.8
Mosses	0.1	0.2	0.1	0.2	0- 0.9
Unknown	2.9	0.7	0	1.3	

[1] Decumbent, evergreen variety

Sitka Black-Tailed Deer—Habitat Relationships

Forest Vegetation and Patterns of Habitat Use

Secondary Succession. The old-growth, commercial forest is characterized by uneven-aged stands that are greater than about 250 yrs old (see Alaback 1980, Franklin et al. 1981) and dominated by western hemlock and/or Sitka spruce with an understory composed primarily of ericaceous shrubs, ferns, and forbs. Dominant trees tend to be massive, and the understory tends to be relatively productive (800 kg ha^{-1}) and rich in number of species (Alaback 1980 and 1982). The successional sequence following windthrow is difficult to characterize, because the degree and frequency of disturbance ranges from scattered trees being blown down or dying to entire stands being blown down at once (Alaback 1980 and 1982). Windthrow of individual, large trees or small groups of trees appears to be the most frequent type of disturbance within the old-growth forest (Brady and Hanley 1984).

Following clearcutting of relatively well-drained sites, shrubs dominate for the first 15-25 years and then are outcompeted by young conifers (Harris 1974, Alaback 1980). Following canopy closure of the young conifer stand, vascular understory species are virtually eliminated for about a century before they begin to become reestablished (Alaback 1982). Availability of forage for deer (i.e., current annual growth of vascular understory species) fluctuates greatly during this successional sequence, ranging from as high as 5,500 kg ha^{-1} at about 20 yr to as low as 0 kg ha^{-1} near 50 yr (Fig. 5). This pattern is similar to that which occurs in the coastal Pacific Northwest (Hanley 1980, Fig. 5), except that the early seral (30 years) levels of shrub biomass and production tend to be much greater in southeastern Alaska, while the mid-seral (30-150 yrs) levels of understory biomass and production tend to be much lower (cf. Long and Turner 1975, Turner and Long 1975, Long 1976, Hanley 1980, Alaback 1980). Also, there is a striking lack of a dominant herbaceous component in early seral clearcuts in southeastern Alaska. For example, current annual growth of herbaceous vegetation in clearcuts of age 8-13 yr in the Cascade Range of western Washington was 2,100 kg ha^{-1} (Hanley 1980), as compared to about 400 kg ha^{-1} in southeastern Alaska (Alaback 1980); respective levels of shrub current annual growth were 1,100 versus 2,400 kg ha^{-1}.

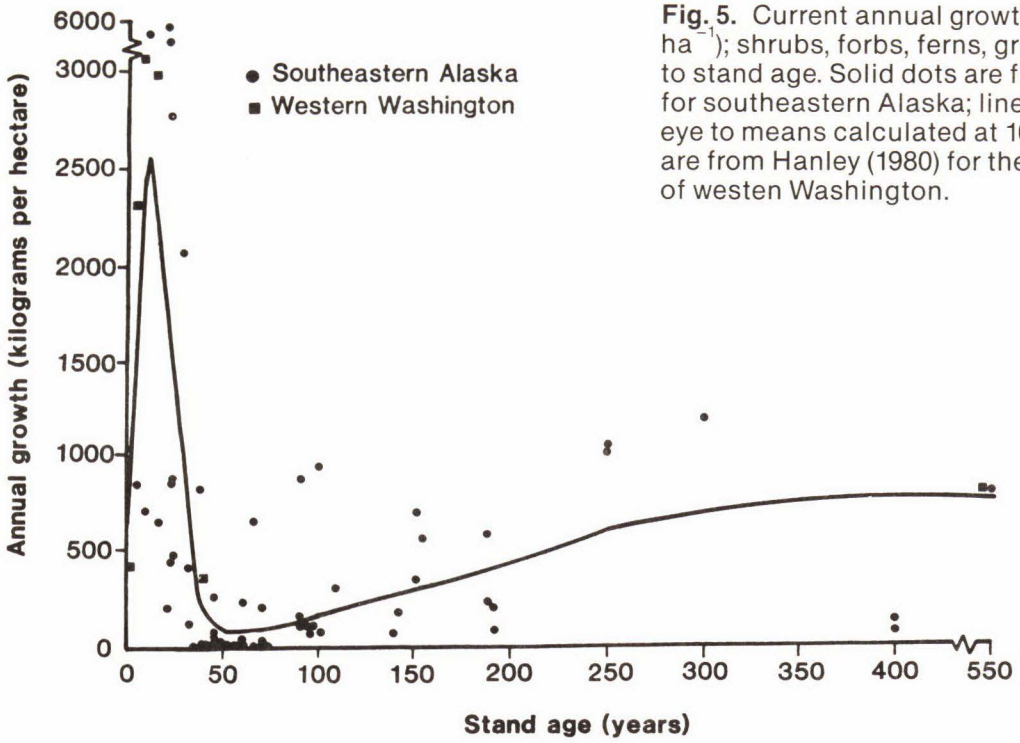
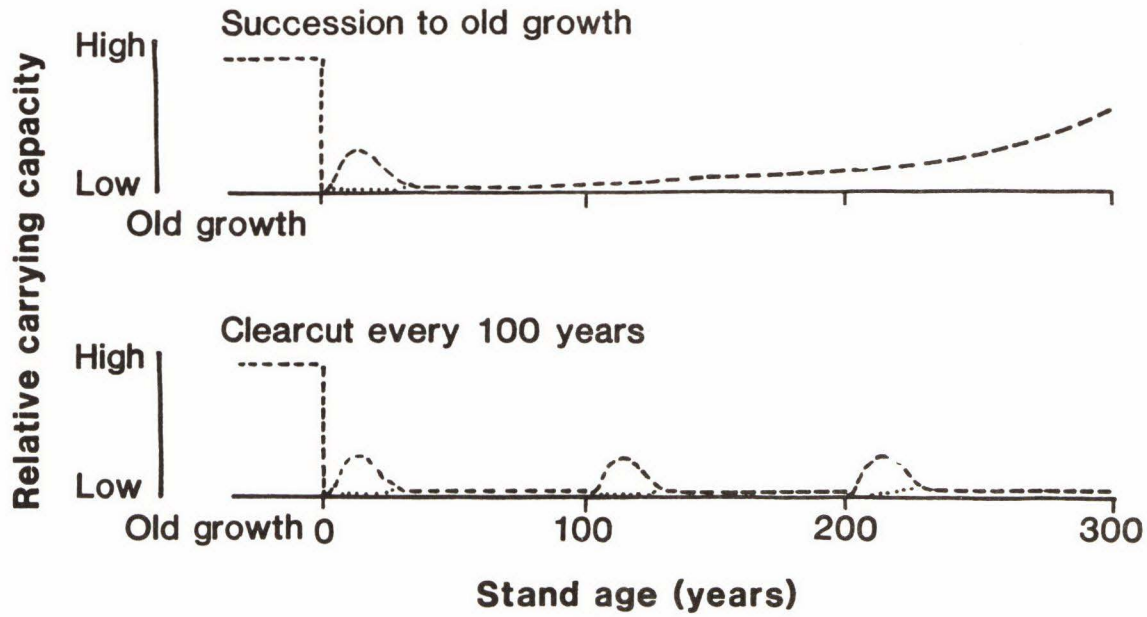


Fig. 5. Current annual growth of understory (kg ha^{-1}); shrubs, forbs, ferns, graminoids) in relation to stand age. Solid dots are from Alaback (1980) for southeastern Alaska; line has been fitted by eye to means calculated at 10-20-yr intervals. X's are from Hanley (1980) for the *Abies amabilis* Zone of westen Washington.

Fig. 6. Hypothesized changes in carrying capacity for deer during succession in western hemlock-Sitka spruce forest in southeastern Alaska. Upper: succession to old growth; lower: clearcut every 100 yrs. In recent clearcuts (dotted line), winter carrying capacity may be reduced to zero by snow (from Wallmo and Schoen 1980).



Habitat Relationships

If a habitat's carrying capacity for deer is directly proportional to its production of forage, then carrying capacity for deer should increase immediately following clearcutting of the old-growth forest and decrease with canopy closure of the second-growth forest (Brown 1961). Besides the quantity of forage produced, however, it is important to consider what forage is available, especially in winter. The frequency, depth, and duration of winter snowpacks are critical factors affecting the relationship between forage production and carrying capacity for deer. Snow accumulates to a much greater extent in recent clearcuts than in forests, thereby reducing the availability of forage and increasing the energy costs of travel for deer (Gates 1968, Jones 1974 and 1975, Fitzharris 1975, Weger 1977, Harestad 1979, Schoen and Wallmo 1979). Under these circumstances, the carrying capacity of the old-growth forest is much greater than that of any earlier seral community (Harestad et al. 1982). The old-growth forest is also important when arboreal lichens are available. Arboreal lichens are important sources of energy for deer during winter but are available in significant quantities only in old-growth forests (Bunnell and Eastman 1976, Bunnell 1979, Rochelle 1980).

Wallmo and Schoen (1980), working on southern Admiralty and eastern Chichagof Islands of southeastern Alaska, examined the use of old-growth and "young-growth" stands by deer. Based on fecal pellet groups deposited during summer and winter, the data revealed that deer used old-growth forest more than they did recent clearcuts and closed-canopy second-growth forest, during both summer and winter (Fig. 6). Virtually identical patterns during winter have been observed on Annette Island on the very southern end of the Alexander Archipelago (Rose 1982). Further south on Vancouver Island, British Columbia, old-growth forest was preferred habitat during winter (Jones 1974 and 1975, Harestad 1979, Bunnell 1979, Rochelle 1980), but recent clearcuts tended to be used more heavily during summer (Harestad 1979), as was the case on the summer range in western Washington (Hanley 1980).

The central assumption of all of these studies is that the use of habitat is roughly proportional to habitat quality (i.e., the capacity of a habitat to produce and/or support deer). This assumption is well founded on theoretical grounds (Lack 1954, Levins 1962 and 1968, Brown 1969, Fretwell and Lucas 1970, Fretwell 1972, Templeton and Rothman 1974, Rosenzweig 1974, Doyle 1975, Orians 1980). On northern Vancouver Island, evidence is mounting that deer populations actually have declined following logging (Hebert 1979), as would be predicted by the models based on habitat use (e.g., Harestad 1979, Wallmo and Schoen 1980).

Variation Within the Forest. Viereck and Dyrness (1980) listed 14 forest overstory types that apply to southeastern Alaska. Only 3 of the 14 types comprise a substantial proportion of the commercial forest lands: (1) Sitka spruce, (2) Sitka spruce-western hemlock, and (3) western hemlock-Sitka spruce (western redcedar). The latter two types intergrade almost imperceptibly with one another. Although Viereck and Dyrness tentatively subdivided these 3 types into 6 community types (Table 6), much work lies ahead in identifying patterns of species associations in southeastern Alaskan forest understories.

Schoen et al. (1981) identified 3 major understory species associations within the commercial spruce-hemlock forests on Admiralty and eastern Chichagof Islands: (1) a blueberry/bunchberry-five-leaved bramble-fernleaf goldthread association, (2) a devilsclub/skunk cabbage-violet-lace flower association, and (3) a single delight-conifer seedlings association. When the individual stands were plotted in relation to principal components, however, no distinct community types were evident, indicating that the species associations were best considered as gradients rather than community types per se (Schoen, Kirchhoff, and Hanley unpublished). The blueberry/bunchberry- five-leaved bramble-fernleaf goldthread association was most common on well-drained sites, whereas the devilsclub/skunk cabbage-violet-lace flower association was most common on wet sites, with devilsclub dominating on shallow, rocky soils with flowing water and skunk cabbage dominating on poorly-drained, mucky soils with standing water. The single delight-conifer seedlings association appeared to be related to dead and down debris, where single delight and conifer seedlings became established above the underlying forest floor. This species association, therefore, appeared to be independent of the other two associations. These analyses are tentative, however, and in need of further work.

Habitat Relationships

Table 6. Partial preliminary classification of southeastern Alaskan forests (after Viereck and Dyrness, 1980). These 3 (of 14) overstory types comprise the majority of the commerical forest lands.

Overstory Type (Level IV)	Community Type (Level V)
Sitka spruce—occupies wet sites, primarily alluvial flood plains	*Picea sitchensis/Oplopanax horridum-Rubus spectabilis/Cornus canadensis*
Sitka spruce-western hemlock—occurs on moist sites	*Picea sitchensis-Tsuga heterophylla/Lysichiton americanum/ Sphagnum* spp. *Picea sitchensis-Tsuga heterophylla/Vaccinium ovalifolium-V. alaskensis-Menziesia ferruginea* *Picea sitchensis-Tsuga heterophylla/Moneses uniflora-Tiarella trifoliata/Mnium* spp.
Western hemlock-Sitka spruce-(western redcedar)—widespread throughout southeastern Alaska	*Tsuga heterophylla-Picea sitchensis-(Thuja plicata)/Vaccinium ovalifolium-V. alaskensis/ Rhytidiadelphus loreus.* *Tsuga heterophylla-Picea sitchensis-(Thuja plicata)/Lysichiton americanum/Sphagnum recurvum.*

Forest overstory influences forest understory through its dominant effects on microclimate and both above- and below-ground resource availability. Understory production tends to be negatively associated with overstory vigor and density, but the relationships between individual variables vary with stand structure (Alaback 1980). In Alaback's (1980) analysis of 62 stands, understory production was negatively correlated with overstory canopy coverage, foliar biomass, and stand volume in young (90 yrs), even-aged, second-growth stands but was positively correlated with mean tree diameter, basal area, and stand volume in mature (90 yrs) even-aged and uneven-aged, old-growth stands. The positive correlations in the mature and old-growth stands were related to the increased spacing between individual, large trees, which was accompanied by an increase in mean tree diameter and volume as stands aged. This is what constitutes the "breaking-up of the canopy" as stands age beyond silvicultural maturity and understory biomass and productivity increase (Bormann and Likens 1979, Franklin et al. 1981).

In southeastern Alaska, patterns of habitat use by deer within the forest have been studied most intensively during winter and early spring, the seasons when deer are most heavily dependent on forests. From these studies (Leopold and Barrett 1972, Bloom 1978, Barrett 1979, Schoen et al. 1979 and 1981, Rose 1982) it is apparent that habitats of greatest value to deer during periods of snow accumulation were moderate- to high-volume, old-growth, western hemlock-Sitka spruce forest with an understory of blueberry/bunchberry- five-leaved bramble. This combination of structural and compositional characteristics apparently resulted in both a high degree of snow interception and snow redistribution by the massive forest canopy, as well as high quality, nutritious forage available in the understory.

During snow-free periods, the relative qualities of various habitats may shift. Herb-layer, evergreen plants (e.g., bunchberry dogwood, five-leaved bramble) continue to be the forage of highest quality, but may be more available in more open-canopied, lower-volume forests than those preferred during periods of snow accumulation (Fig. 7).

Wet sites with an understory dominated by devilsclub or skunk cabbage tended to receive less use during winter than did well-drained sites with understories dominated by huckleberry (Schoen et al. 1981). During early spring, however, skunk cabbage is one of the first species to produce new vegetative growth above ground, and deer use the succulent new growth heavily (Klein 1965). Forest patches where skunk cabbage is abundant receive a high degree of use by deer during this relatively brief but important time.

Patterns of habitat use by deer within the forest shift, therefore, with changing snow conditions and plant phenology through the winter and spring. Although moderate- to high-volume, old-growth, western hemlock-Sitka spruce forest with an understory of blueberry/bunchberry-five-leaved bramble may be the most important kind of habitat for deer during deep snow accumulations, other kinds of forested habitat may be of greater value during snow-free periods. Variety of habitat on the winter range is an important aspect of habitat quality for deer.

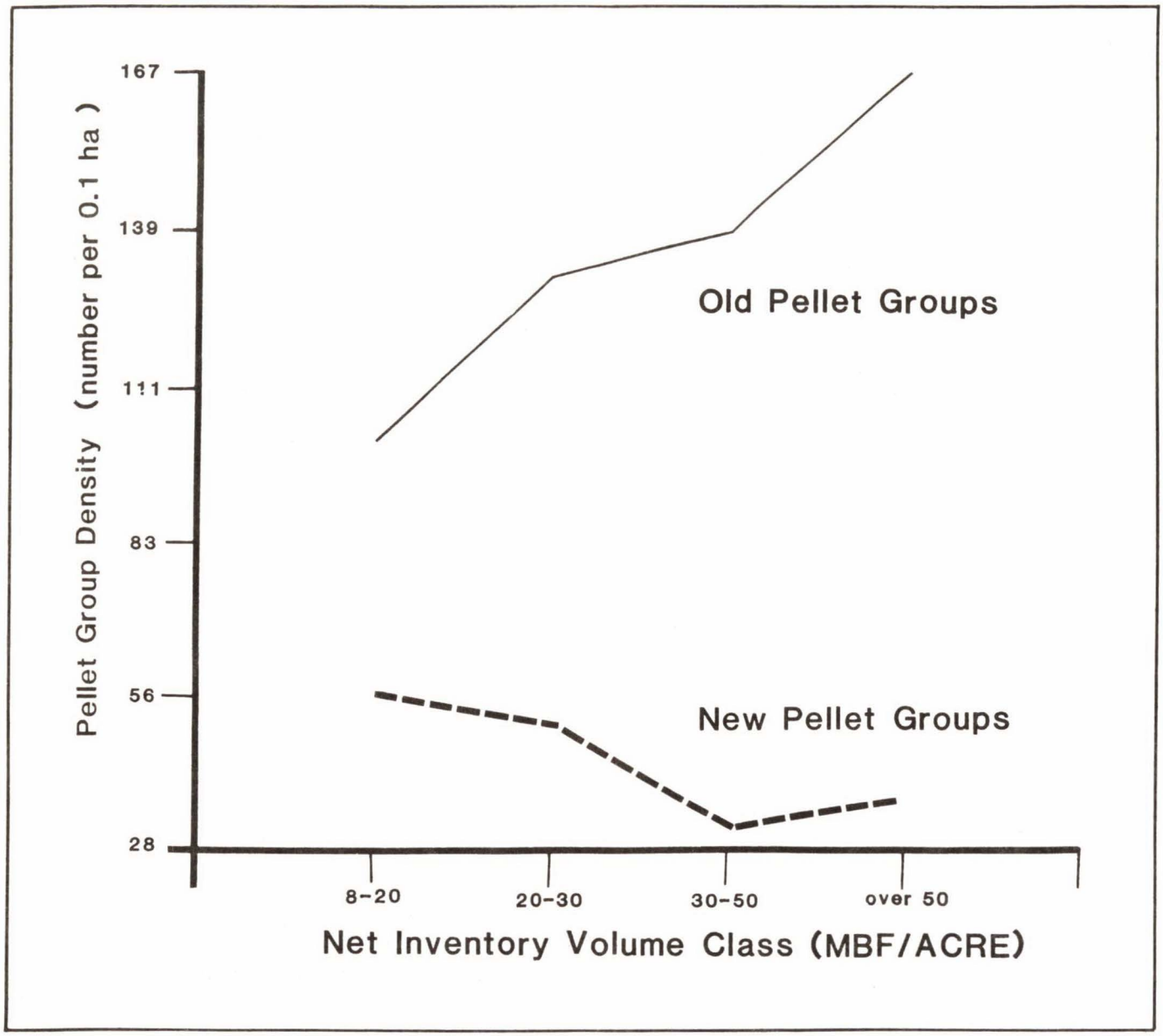


Fig. 7. Relationships between net timber volume (thousand board feet per acre) and mean density of old and new pellet groups. Data were from 49 0.4-ha plots in old-growth forest, Tenakee Inlet, 1980. Old pellets represent winter use; new pellets represent spring use (from Schoen et al. 1982).

Habitat Relationships

A Benefit-Cost Model of Habitat Quality. Why might old-growth forest be preferred to snow-free recent clearcuts in southeastern Alaska, even during summer? Superficially, this pattern of habitat use appears to be contradictory to that of black-tailed deer in more southern latitudes. Wallmo and Schoen (1980) suggested that logging slash may be the primary factor restricting deer use of recent clearcuts during snow-free periods. An alternative, based on data presented by Billings and Wheeler (1979), Van Horne (1982), and Rose (1982) indicating that nitrogen content of understory plants is greater in old-growth understory than in clearcuts, is that deer use of clearcuts is lower because of differences in forage quality. A third alternative is that deciduous shrubs quickly form such dense stands in southeastern Alaska, that any benefits derived from increased forage availability in clearcuts are more than offset by increased energy costs of travel in the areas.

All three of these alternative hypotheses could be correct and interactive. This can be illustrated in a simple, generalized model of habitat selection (Fig. 8). In this model, as the biomass of herb- and shrub-layer vegetation increases, intake of metabolizable energy increases rapidly at first and then levels off at a saturation level. Also, it is assumed that energy costs of locomotion are low and relatively monotonic at low and medium levels of shrub biomass but increase exponentially at high levels of shrub biomass. Habitat quality for deer is the difference between the intake and cost functions, with the optimal habitat being the level of shrub biomass where intake minus cost is maximum. There are also two extremes where foraging costs exceed foraging benefits—one at very low and one at very high levels of shrub biomass. At the points where the two functions intersect, costs are equal to benefits.

Even-aged second-growth, uneven-aged old-growth, and recent clearcut habitats in southeastern Alaska should have low, medium, and high levels of shrub biomass (Figure 8). If this is the case, as it appears to be, snow-free clearcuts in western Washington and Oregon, with lower peak levels of shrub biomass than those in southeastern Alaska are of greater value to deer than are those in southeastern Alaska.

Support of this model comes from the convex parabolic curves that Willms (1971:85-96) observed for the relationship between deer use and shrub canopy coverage on Vancouver Island. Willms noted that deer pellet densities within clearcuts were positively correlated with shrub cover at low and medium levels of shrub cover, but they were negatively correlated at high levels of shrub cover. This relationship would be predicted from Figure 8.

The benefit and cost functions are dependent on more than forage availability and shrub biomass. Forage quality is important (Moen 1973, Wallmo et al. 1977), as are relationships involving thermal energy exchange (Moen 1973, Beall 1974), logging slash (Lyon 1976, Lyon and Jensen 1980), and snow depth (Gilbert et al. 1970, Drolet 1976). These factors can be incorporated into the model by altering the benefit and cost curves.

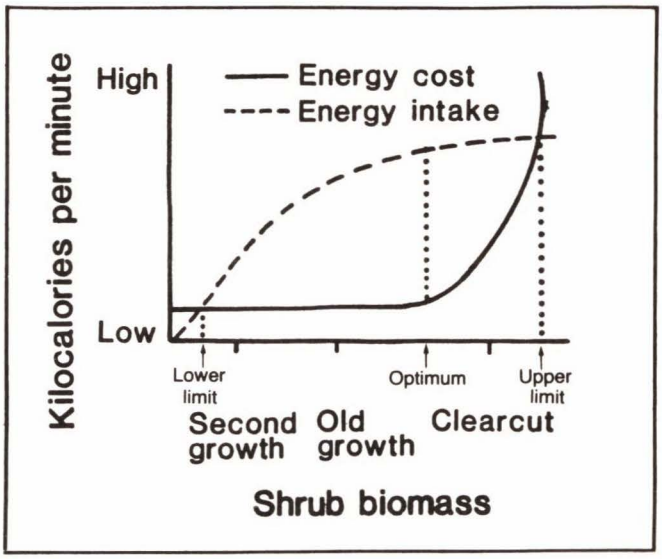


Fig. 8. A foraging benefit-cost model of habitat selection. Deer should prefer habitat patches where the difference between the energy intake function (dashed line) and energy cost function (solid line) is greatest. There is an optimal level of shrub biomass (or range of levels) as well as a lower and upper limit of habitat "suitability" (where energy intake is not less than energy cost).

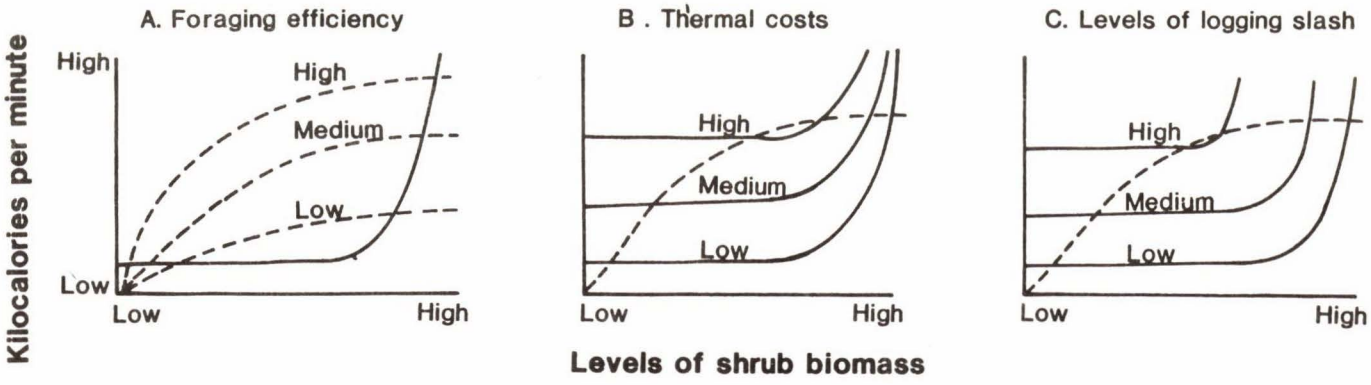


Fig. 9. Effects of varying foraging efficiencies (a), thermal costs (b), and logging slash (c) are modeled by varying the appropriate energy intake or cost function.

Differences in forage quality affect the intake function. As forage quality increases, the net rate of intake of metabolizable energy (i.e., foraging efficiency) increases (Fig. 9a). This results from a greater nutrient value per unit weight of forage and a greater passage rate of ingested forage. With the latter, there is an opportunity for more bites per unit time and/or a greater amount of time for selectively choosing bites (Hanley 1982b). As forage quality increases, the difference between the energy intake and cost functions increases. The reverse is true of decreased forage quality.

Differences in the thermal environment might also affect the foraging cost function. As thermal energy losses from the deer to the environment increase so too must the energy expended by the deer to maintain homeothermy (Fig. 9b). Costs of thermal energy exchange are additive to the foraging costs (Moen 1973) and result in a raising or lowering of the cost curve with little or no effect on its shape. As thermal energy costs increase, the difference between the energy intake and cost functions decreases.

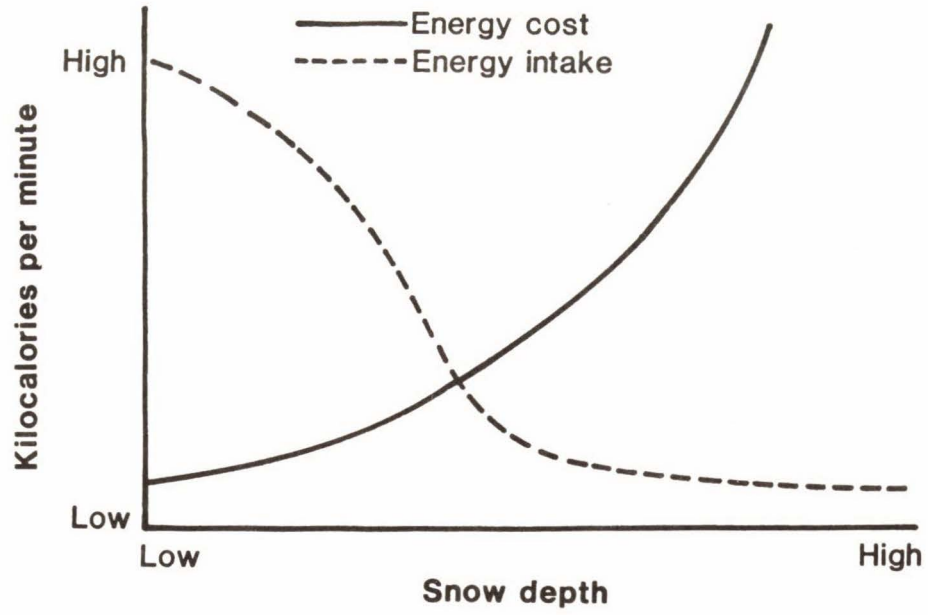
Depth and amount of logging slash also affect the foraging cost function. If the effects of logging slash and shrub biomass are interactive (i.e., each exaggerates the effect of the other), the result is both a raising of the cost curve and a sharpening of its inflection with increases in logging slash (Fig. 9c). As the amount of logging slash increases, the difference between the energy intake and cost functions decreases.

While changes in forage quality, thermal environment, or amount of logging slash will affect the range of habitats that are suitable for deer, only changes in factors that are interactive with shrub biomass (in this case, logging slash) will affect the level of shrub biomass considered to be optimal.

The effects of snow are more complicated. As snow depth increases, it simultaneously decreases forage availability and quality and increases foraging costs. In general, energy requirements increase exponentially with snow depth while food availability decreases (Fig. 10). If the snow is capable of supporting a deer's weight, then it effectively reduces the level of shrub biomass and the amount of slash. It reduces forage quality by burying the herb-layer plants but may not add to the energy costs of travel, depending on the depth to which the deer sinks. The overall effect of snow is to restrict the range of suitable habitats and to lower the quality of all habitats.

The optimization problem faced by the deer is one of choosing the combination of habitat patch and diet where the difference between the foraging benefit and cost functions is maximized. A deer's choice of habitat patch will determine the foraging costs; the available forage and the deer's choice of diet within that patch will determine the energy intake. The difference between a deer's foraging benefit and cost functions determines the deer's net energy balance.

Fig. 10. An energy benefit-cost model illustrating the effect of snow depth on energy intake cost while foraging (from Harestad et al. 1982).



Home Range

To a large degree, an individual deer's movements are confined to a limited area known as its home range. Home ranges, especially of females, apparently are learned by deer during their first year or two of life from association with their mothers (Dasmann and Taber 1956, Nelson and Mech 1981). Fidelity to these home ranges can be so great that deer have been known to starve to death on their traditional home range rather than travel a few kilometers to abundant forage (Dasmann and Taber 1956). Among seasonally migratory deer, summer home ranges are usually larger than winter home ranges, and bucks tend to have larger home ranges than do does; also, bucks are more mobile and more likely to establish new home ranges than are does (Dasmann and Taber 1956, Robinette 1966, Miller 1970, Nelson and Mech 1981). For an individual deer, home range determines what habitats are available, and, to a large degree, tradition determines the distribution of deer over the landcape (Nelson 1979). Since quality of habitat is not uniform over the landscape, however, some deer fare better than others (Taber and Dasmann 1957).

Home ranges of telemetered deer in southeastern Alaska (Schoen et al. 1981, Schoen and Kirchhoff 1985) are comparable in size to those reported for Columbian black-tailed deer in the Pacific Northwest (Miller 1970, Harestad 1979, Hanley 1980). Much variation exists between individual deer, probably reflecting differences in early experience as well as habitat composition of their home ranges (Schoen et al. 1981). About 75% of the telemetered Sitka black-tailed deer captured on the winter range and monitored year-round by Schoen and Kirchhoff (1985) made distinct seasonal migrations between winter and summer ranges; the others were year-round residents of their winter ranges. Deer utilized similar summer and winter home ranges between years, suggesting strong fidelity to home ranges (Schoen and Kirchhoff 1985). "Migratory" deer generally summer at relatively high elevation habitat, while "resident" deer remain in the low elevation habitats year-round. This phenomenon is common in the coastal Pacific Northwest with Columbian black-tailed deer as well (Taber and Hanley 1979, Harestad 1979).

Seasonal Movements. In early spring, most deer in southeastern Alaska are still on the winter range usually between sea level and 300 m (Klein 1965, Schoen et al. 1981). Upper elevational limits may vary from 100 m during years of heavy snow accumulation and/or on northerly exposures to 600 m during light snow and/or on southerly exposures. As the snowline recedes, deer movements expand, and greater use is made of areas with new, green vegetation. By late spring, high quality forage is abundant and migratory deer move to or near their summer ranges. Spring home ranges of 13 telemetered deer reported by Schoen at al. (1981) ranged from 30 to 12,369 ha and averaged 1,521 ha. The large size of spring and fall home ranges reflect the movements of migratory deer between winter and summer home ranges. Straight-line distances between summer and winter ranges for radio-telemetered, migratory deer have been observed between 1.6 and 72.5 km (Schoen et al. 1981). Most deer probably move less than 10 km between winter and summer home ranges. In general, spring can be considered a transition period between summer and winter ranges for migratory deer. In comparison, for resident deer, some of which spend their whole year and perhaps their entire lives within 200 ha, only localized shifts in habitat use occur. Parturition occurs in late May and early June, most likely in lower elevation forested habitat.

During summer, migratory deer on the mainland and larger islands have access to abundant, high quality forage in alpine and subalpine habitats (Klein 1965). These habitats are preferred by migratory deer during this season (Schoen et al. 1981). Mean summer home range of 37 telemetered deer reported by Schoen and Kirchhoff (1985) was 79 ha (SE=10.2). Home ranges were distributed from sea level (resident deer) to over 1,000 m (migratory deer).

Fall home ranges of 12 telemetered deer reported by Schoen et al. (1981) averaged 505 ha and ranged from 64 to 1,307 ha. Migratory deer continue to utilize alpine and subalpine habitats through early fall. After the first heavy frosts when much of the herbaceous forage is killed in the alpine and subalpine, however, deer move into the upper forest. They may remain at these higher elevations throughout fall unless snow begins to accumulate. The elevational distribution of deer between years and within years is highly variable. Some deer move up and down with a changing snowline; others move to lower elevations following the first snow and stay there; while others may remain in areas where snow accumulations exceed 30 cm (Schoen et al. 1979 and 1981). The rutting period occurs from late October to early December.

Winter through early spring is the period of greatest year to year variation in deer distribution. It also is the most limiting period for forage resources and the time of highest mortality. The mean winter home range of 47 telemetered deer was 79 ha (SE=15.6) (Schoen and Kirchhoff 1985). In some years, elevations below 300 m are nearly snow-free throughout the winter. In other years, snow may accumulate below 150 m for 4 to 5 months with extensive snow at sea level. Early winter snow accumulations seldom remain long at lower elevations because of the strong maritime influence in southeastern Alaska. As rain melts the snow, many migratory deer which moved to lower elevations after the first snow again move into the higher forest, often as high or higher than 600 m (Schoen et al. 1981 and 1982). Throughout the winter, both migratory and resident deer move up and down within their home ranges depending on changing snow levels. It appears that many deer winter as high as snow conditions allow (Olson 1952, Merriam 1968, Barrett 1979, Schoen et al 1981). During the winters of 1978 through 1982, the mean elevation of telemetered deer on Admiralty Island was 124 m (SE=6.2) with migratory deer wintering higher than resident deer (Schoen and Kirchhoff 1985). All telemetered deer relocations averaged 0.6 km (SE=0.1) from the beach and the home range centers of 52% of the deer were beyond 0.4 km from the beach (Schoen and Kirchhoff 1985). Historically important deer range in southeastern Alaska was considered to be below 150 m elevation or 0.4 km from the coast. When the snow is deep even at sea level, the beach and beach-fringe forest becomes the last refuge for many deer. In less severe conditions, the best winter habitat may be many kilometers from the beach.

Habitat Relationships

Influence of Deer on Vegetation

Deer can affect vegetation through selective consumption of plant parts and individuals and by trampling. As a result of deer use, palatable woody stems and succulent forbs with meristematic tissue located above the ground surface tend to decrease, while graminoids and forbs with meristematic tissue at or below the ground surface may increase (Hanley and Taber 1980). If the deer are abundant, they may create an "open" appearing landscape (Hanley and Taber 1980).

Deer browsing severely altered the vegetation on Coronation Island in southeastern Alaska (Klein 1965). Deer use resulted in hedged growth forms of early blueberry, red huckleberry, red elderberry, and even western hemlock and Sitka spruce. Klein believed that excessive use by deer had resulted in the elimination of important winter and summer forage species on the island. Similarly, high population levels of introduced Sitka black-tailed deer on the Queen Charlotte Islands, British Columbia, have affected the vegetation so heavily that foresters are concerned about the future regeneration of western redcedar, Alaska yellow cedar, western hemlock, and even Sitka spruce (Pojar et al. 1980). Deer browsing damage to young Douglas-fir has been a problem for foresters in the Pacific Northwest for many years (Cowan 1945, Crouch 1981). Moderate levels of deer browsing on shrubs, however, may reduce competition and be beneficial to young conifers (Crouch 1974, Hanley and Taber 1980).

As high quality forages decrease, deer must consume lower quality forages, resulting in decreased diet and habitat quality (Taber and Dasmann 1957, Klein 1965, Carpenter et al. 1979). The effects of decreased diet quality on Sitka black-tailed deer were demonstrated in Klein's (1962, 1964, 1965) comparison of deer populations and their habitat on Woronkofski and Coronation Islands in southeastern Alaska. For a variety of reasons, including mild winter weather and the absence of wolves on Coronation Island, deer populations there were believed to commonly exceed the normal carrying capacity of their habitat, resulting in a decrease of high quality forages. In contrast, although deer on Woronkofski Island had access to a greater proportion of alpine and subalpine habitat in the summer, they were subject to more severe winter weather and wolf predation and exceeded the carrying capacity of their habitat less often than did deer on Coronation Island. Deer populations on Coronation Island had lesser body weights and growth rates, a lower ratio of fawns to adult females, an older average age, a less even sex ratio, and a higher natural mortality of young animals than did those on Woronkofski Island. These attributes are characteristic of lower quality diet.

Management Implications

The conversion of uneven-aged old-growth forest to even-aged stands through timber management results potentially in a great loss of carrying capacity for Sitka black-tailed deer. Closed-canopy, second-growth stands comprise about 75% of a 100-year stand rotation and are virtually nonproductive for deer. Although recent clearcuts (25-years-old) are highly productive of plant biomass, this biomass is largely comprised of conifer seedlings and woody shrubs which have relatively low value to deer in winter. Compounding the problem, in certain areas and/or years, is the effect of snow which can render much of the forage produced in clearcuts unavailable. Present indications are that clearcut logging in southeast Alaska generally will reduce the carrying capacity of deer winter range and result in a long-term reduction in deer numbers.

Many factors must be considered when developing forest management prescriptions for Sitka black-tailed deer. Specific local information concerning natural vegetation, climate, elevation, topography, and predation and their interactions must be considered. What is considered an optimum management practice in one area, may not be optimum in another. The response of local deer populations to forest management practices will differ depending on environmental circumstances (e.g., local weather, topography, habitat availability, predation) which vary geographically and over time.

Although management prescriptions must be based on local circumstances, there are general principles which can be applied universally. Understanding the functional relationships between deer and their habitat will help in management. Physiological requirements of deer under various environmental conditions can be useful in defining what habitats are required and optimal. Optimum habitat throughout the range of Sitka black-tailed deer cannot be defined in terms of specific structural or compositional features. The "optimal" elevation, stand volume, or understory species composition, for example, varies with environmental circumstances and is not a fixed "habitat requirement" of deer. Beyond the functional relationships, the following guidelines may be helpful in focusing attention on specific features of habitat.

Critical Winter Range

The concept of "critical winter range" is commonly used and means habitat that is of great importance for survival and is in relatively short supply during periods of severe winter weather (in southeastern Alaska, periods of deep snow accumulation). Critical winter range is the optimal habitat under climatic conditions that are most responsible for winter mortality of deer. It is not optimal habitat under all winter conditions and, alone, it may not even be adequate to support deer throughout an entire winter. Other habitats also are important for relieving browsing pressure from critical winter range during periods when snow is not deep.

From a deer's perspective, there probably are three thresholds of snow depth. The first is the depth at which evergreen forbs and herb-layer shrubs become buried, approximately 10 cm. The second is when the depth to which deer sink in the snow exceeds front knee height (approximately 25-30 cm) and energy costs for locomotion increase greatly (K. L. Parker and C. T. Robbins personal communication; also see Fig. 2). The third threshold is the point at which tall shrubs become buried. Beyond that, a deer's diet would consist almost entirely of low quality conifer foliage, and its energy costs for locomotion would be extremely high. Crusting of the snowpack can affect sinking depth greatly, but even with a good crust, buried forage remains a problem. For management purposes, therefore, snow depths which cover herb-layer forages (5-10 cm) should be considered significant and depths greater than 25-30 cm probably should be considered "deep snow."

Weather. The winter weather in southeastern Alaska generally varies from frequent, high snowfall conditions in the northern part of the Alexander Archipelago to less frequent, lower snowfall conditions in the southern portion of the Archipelago. A parallel, smaller gradient may exist from east to west in the Archipelago as well. Average winter temperatures conform to the above patterns and are generally more consistent from year to year than is snowfall. Severe winters, when snow accumultions at sea level exceed 30 cm for four or more months, occur throughout the Archipelago from time to time.

Management Implications

Topography. The degree of slope influences snow depth by its effect on the ratio of surface area to horizontal area. Assuming snow falls more or less vertically, with increasing slope steepness, a given amount of snowfall is distributed over an increasingly large area, resulting in a greater proportion of the snowpack being exposed to air and radiant energy (Fig. 11). Similarly, but on a microtopographic scale, large dead and down woody debris may increase ground surface area. Moss-covered logs and stumps and broadly spreading roots of trees, when providing substrate for understory plants, raise some growing surfaces above the ground level and distribute snow over a larger area. All other things being equal, the rate of snow ablation will be proportional to surface area exposed.

Southerly aspects are exposed to much more potential solar radiation than are northerly aspects, and radiation increases with steepness of slope on southerly aspects and decreases on northerly aspects (Fig. 12). Snow ablation varies accordingly. Possibly, steep southerly slopes are usuable longer in fall, winter, and spring than are shallow southerly slopes or any northerly slopes. Considering the low sun angle at northerly latitudes during winter and the steep topography of southeastern Alaska, shading of the slope by adjacent mountains may be another factor to consider (Fig. 13). Unshaded, southerly-facing beaches and slopes may provide more suitable habitat than shaded ones.

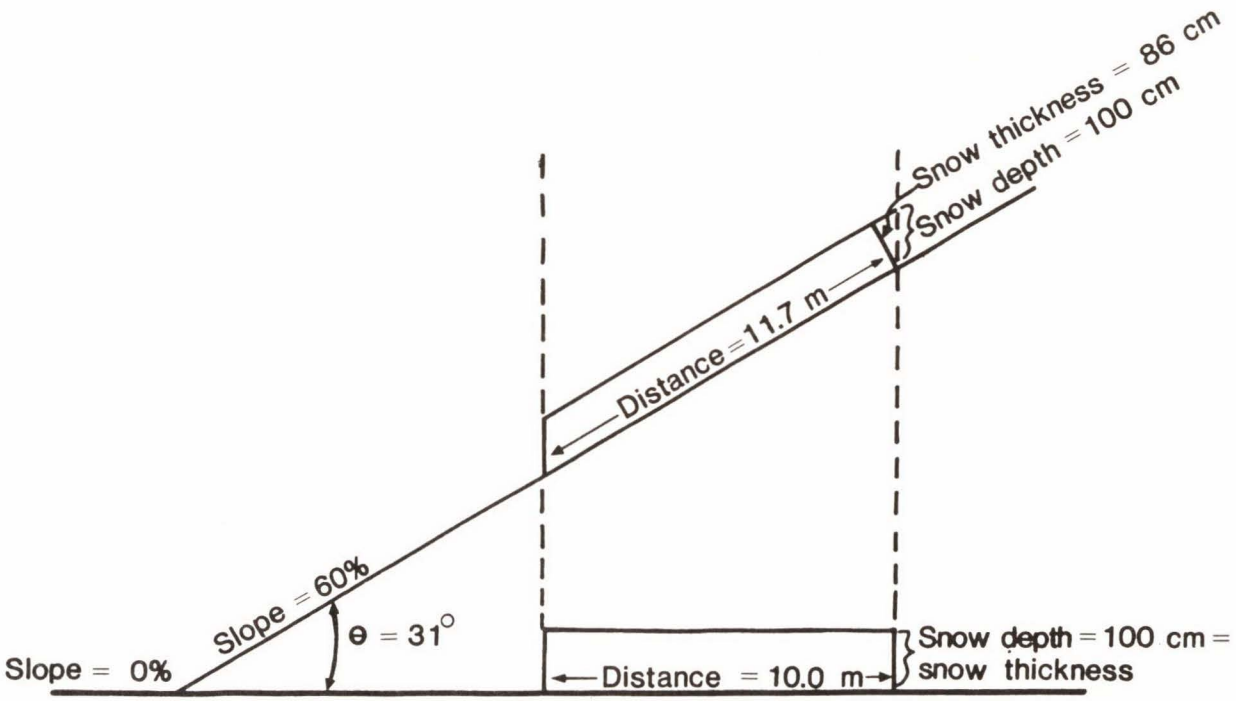


Fig. 11. The effect of slope angle on snow thickness. Other things being equal, snow thickness is less on steep slopes than on moderate slopes or level areas because of a greater amount of ground surface area per unit area of vertical projection. A slope of 60 percent (31°) has a ground surface area 1.17 times that of a level area; hence, its snow thickness is 86 percent as great as that of the level area. It's snow depth, however, is the same as that of the level area.

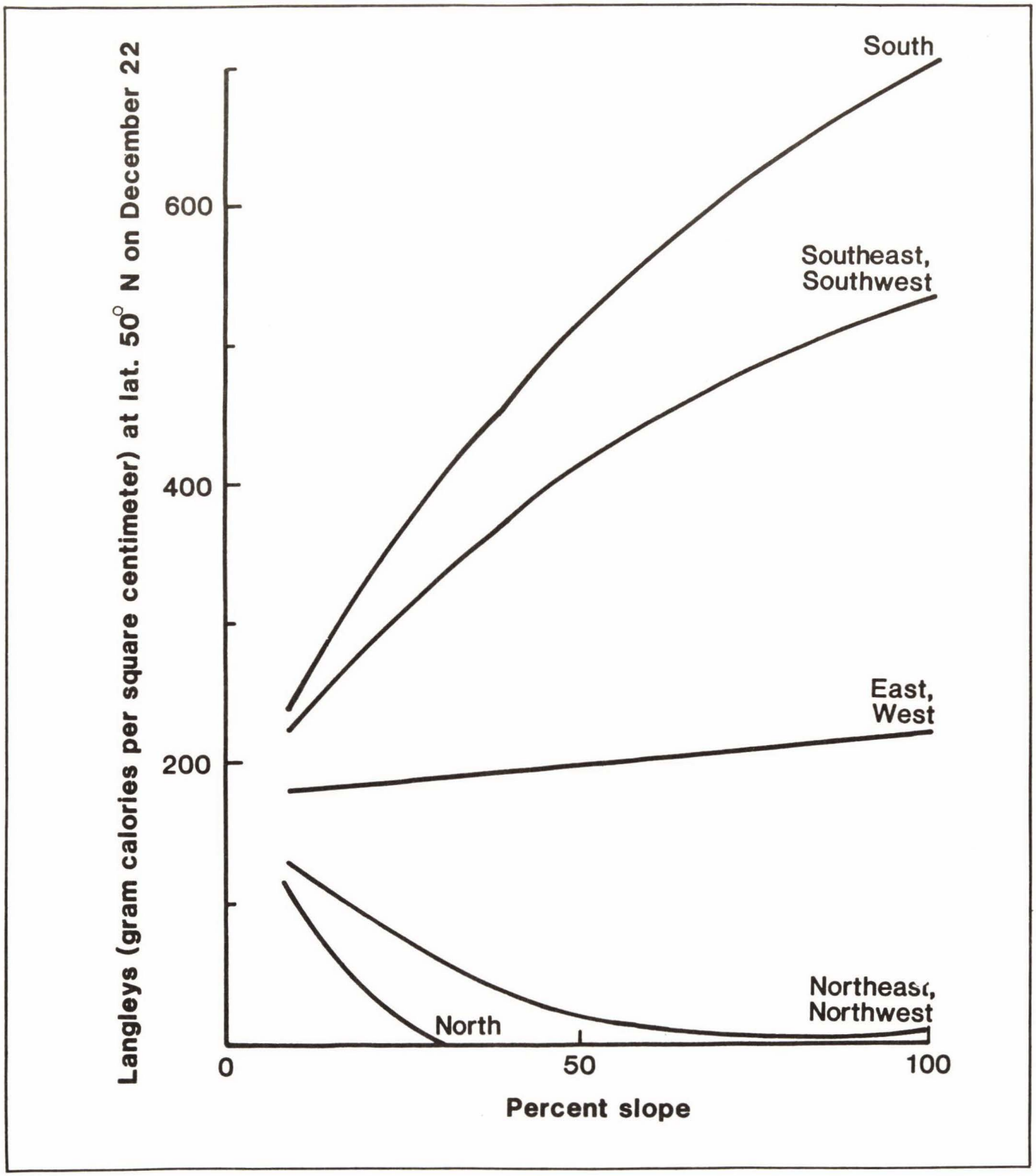
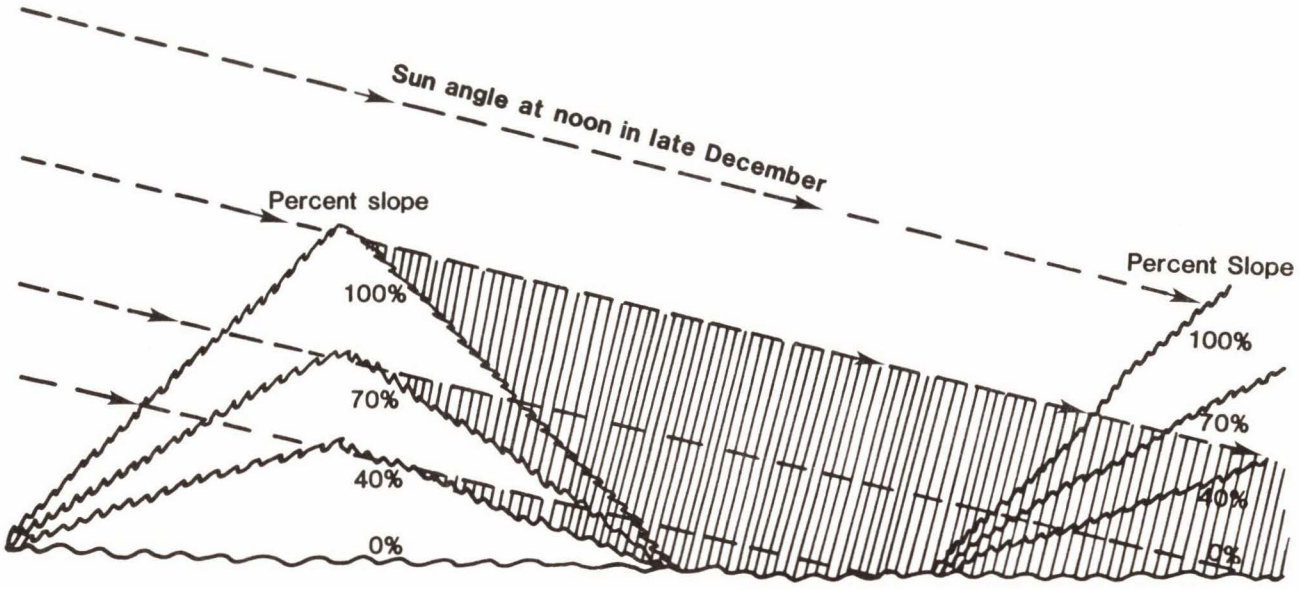


Fig. 12. Effect of slope and aspect on potential solar irradiation.

Management Implications

Fig. 13. Effect of slope, aspect, and shading on solar irradiation of forest habitat. Logging is normally restricted to slopes 70 percent.



Vegetation. Two features of forest vegetation that are of greatest importance for critical winter range are (1) a productive understory of high quality forage and (2) an overstory which intercepts and/or redistributes sufficient snow that understory forage remains available to deer. On Admiralty and eastern Chichagof Islands, these conditions were met most satisfactorily by low to mid-elevation (300 m), moderate to high-volume (30-50,000 board feet per acre), old-growth, hemlock-spruce stands with a canopy cover of about 60-80% and with an understory dominated by blueberry, bunchberry, fernleaf goldthread, and five-leaved bramble (Schoen et al. 1981). Even at moderate snow depths (10-25 cm), these conditions seem to provide some access to highly nutritious evergreen forbs and herb-layer shrubs beneath large trees. At greater snow depths (30 cm), primarily woody browse is available and blueberry is important. The availability of lichen litterfall which occurs primarily in old growth, also may contribute greatly to the quality of critical winter range (Rochelle 1980).

Predation. Wolf predation may be a significant factor controlling deer populations in southeastern Alaska (Klein 1981). This may be most important in years of heavy snowfall and when winter range is limiting. The advantages to deer of generally more moderate winters in the southern portion of the Archipelago may be partially offset by the effects of wolf predation in severe winters when deer are concentrated on the winter range. Although little is known about deer-wolf relationships in the region, wolf predation likely slows the recovery of deer populations after severe-winter die-offs. Theoretically, if the fecundity of a deer population declines below certain threshold levels, a rapid decline in deer density is likely to result, with predation as the proximate cause (Van Ballenberghe and Hanley 1984). Practices of forest management which lower the carrying capacity of the habitat can initiate population declines. Management to maintain habitat and prevent deer declines seems more logical than trying to reverse population trends with wolf control after they occur (Van Ballenberghe and Hanley 1984).

Habitat Protection

Habitat Variety. In managing the forest for deer, it is important to consider land areas other than the moderate to high-volume stands that provide valuable habitat during periods of heavy snow accumulation. Variety of habitat on the winter range is important. Low-volume, open-canopied stands produce abundant understory and are important range in the absence of snow. Much of the forest land in southeastern Alaska is of low timber volume and/or on steep slopes and currently not harvestable. These stands could provide suitable habitat for deer during snow-free seasons. The moderate to high-volume, old-growth forest is a much smaller part of the total forest area and is of concern in timber and deer habitat management, especially in areas of frequent, high-snowfall winters. Recognizing that deer can utilize a variety of habitats on their winter range, depending on snow conditions, the manager faces the task of determining the size and arrangement of areas to be cut and retained, and the timing of entries into an area, so that deer populations can be sustained at desired levels. Habitats deemed most critical and in short supply should be well represented in the retention area, whatever the size and arrangement. Eliminating an area of critical winter habitat could have a far greater effect on deer populations than eliminating an equal area of some other habitat (Schoen et al. 1984).

Size, arrangement and timing of clearcuts and retained areas. Size, arrangement, and timing of clearcuts and retained-areas largely determine the variety of habitat that an area will have. Optimal sizes and placement for deer are related to the size of deer home ranges (Taber and Hanley 1979). The strong fidelity of deer to established home ranges means they are unaware of habitat conditions outside their home range. In planning the cutting sequence, it is important to spread the cutting over the entire elevational gradient. Clearcutting that begins at the lower elevations and moves upward results in a seral stage gradient which is superimposed directly on the elevational gradient and severely limits the deer's options for finding quality habitat during winter.

Concerning size and location of retained areas, one management option is to retain scattered blocks of old-growth critical winter habitat within clearcuts or second-growth stands. This may concentrate deer, however, leading to range deterioration and/or increased predation (Schoen et al. 1984). Additionally, edge trees of the retained areas may suffer increased windthrow and decrease the area of desired habitat. Whereas "edge" between forest and cut-over areas is widely believed to benefit deer, in southeastern Alaska, Kirchhoff et al. (1983) found no increased winter use along forest-clearcut edges. Both the deer concentration and the windthrow problems could be minimized by retaining patches of critical range within a surrounding block of low-volume or non-harvestable forest. This would provide a variety of winter habitat within the home range of deer and at the same time preserve wind-firm boundaries for stands of critical winter habitat. Deer with home ranges outside the protected critical winter range would not know of its existence, thus minimizing problems of concentrated use.

Another option is to cut heavily in certain management areas and defer entry for timber harvesting in others. For those deferred-entry areas, there will be greater flexibility for management in the future when deer-forest relationships are better quantified. On the other hand, habitat variety and management flexibility is reduced in the heavily cut areas. Managers would need to consider specific factors of the local situation, such as present and future amounts and locations of various habitats, weather, topography, and desired levels of populations when dealing with these trade-off values in this management option. Schoen et al. (1984) discussed the advantages and recommended retention of forest land, which, as much as possible, preserves the original distribution, juxtaposition, and diversity of habitat existing prior to timber harvesting.

The relative importance of retaining areas of old-growth forest will vary with the unique composition of each management unit and the desired population levels of deer. In the Pacific Northwest, where the prevailing climate is mild and deep snow accumulations are rare and in short duration, a mosaic of young clearcuts within even-aged, second-growth forest provide suitable winter range for sustaining moderate population levels of deer. This might be appropriate management for the Queen Charlotte Islands, for example. Wolves are not present on the islands and deer populations would be expected to increase rapidly after an occasional severe-winter die-off.

Management Implications

Beach fringe forest. In determining the size, shape and location of retention areas, special consideration should be given to the beach fringe forest. This is the last refuge for deer moving downslope during periods of deep snow accumulation. If deep snows do not persist for long, the beach fringe forest can provide temporary, but critical refuge. It could not sustain large numbers of deer for prolonged periods. Furthermore, if the beach fringe forest is separated from other habitat by extensive recent clearcuts, deer may be confined to the fringe because of deep snow and slash in the clearcuts above it. By cutting in areas over an entire elevational gradient, or by regularly leaving blocks of timber adjacent to the beach fringe forest, the potential confinement problem might be alleviated.

Habitat Enhancement

In recent clearcuts and closed-canopy, second-growth stands, silvicultural practices of forest residue reduction and thinning offer some alternatives for deer habitat improvement. These practices address the problems of increasing forage quality, increasing forage abundance and availability, and improving accessibility.

Residue reduction. In southeastern Alaska, because of the high incidence of defect and the difficulties of harvesting in steep, rocky terrain, there is considerable slash left in clearcuts, even though the amount of slash has been reduced in recent years. Through further increased timber utilization and clean-up of logging slash, accessibility for deer in clearcuts free of snow might be improved. Although the intention might be good, mechanical removal of unutilized material may increase soil disturbance which may stimulate alder or other competitors of conifer seedlings (Ruth and Harris 1979). Burning offers another alternative but is poorly suited to the cool, wet conditions in southeastern Alaska. Broadcast burning would likely reduce shrubs, delay conifer regeneration, and favor herbs. This might improve forage quality and prolong the useful life of clearcuts for deer during snow-free periods. Nitrogen losses through volatilization and leeching may have negative consequences.

Thinning. Densely stocked, closed-canopy, second-growth stands that develop 25-30 years following clearcutting and persist throughout the rotation provide very little if any forage for deer. Precommercial thinning in young stands and commercial thinning of selected trees from older stands may be effective silvicultural practices for deer habitat improvement. In application, the thinning would need to open the stand to increase forage production and quality, and to develop tree crowns capable of intercepting and redistributing snowfall so that forage remains available.

Alaback and Tappeiner (1984) found that tree seedlings and *vaccinium* seedlings respond best to thinning, but on most plots tree seedlings increased productivity at the expense of herbs and shrubs. How significant thinning may be to improving deer winter range will depend on how quickly forest canopies close after thinning and what influence a secondary *Tsuga* canopy created by heavy thinning will have on the understory (Alaback and Tappeiner 1984).

Thinning of dense stands will result in large volumes of slash that might need to be piled or disposed of so it does not inhibit forage production or deer accessibility. Specific thinning recommendations to accomplish these habitat enhancement purposes are not available (Kessler 1982).

Research Needs

Forest and wildlife managers need a means of quantitatively evaluating habitat quality for deer. Relationships between forest understory, overstory, and site need to be understood to predict understory species composition and productivity. Similarly, the chemical composition and nutritional value of forages need to be determined. Relationships between forest overstory, snow interception, and the availability of understory are very important. The metabolic requirements of deer and how they relate to diet selection and habitat selection also are major factors. The theoretical framework for integrating these relationships into a quantitative model has been outlined in the preceding review and elsewhere (Harestad et al. 1982, Hanley unpublished problem analysis). A model based on functional relationships and driven by local climate and site factors would provide an objective means of evaluating habitat quality throughout the range of Sitka black-tailed deer.

In the short term, however, the most glaring lack of information concerns deer population sizes and productivity. Although habitat preferences of deer have been demonstrated, population dynamics have not been studied. No data exist concerning the effects of logging on population sizes, densities, or other demographic parameters of Sitka black-tailed deer. A major reason for the lack of such information is that in habitats of dense forest, steep topography, and highly variable winter climate, it is extremely difficult to census deer populations. Nevertheless, an adequate censusing technology is a necessity for monitoring changes in deer populations and for testing the predictions of theory.

As logging of old-growth forest continues, an increasing proportion of deer habitat, especially winter range, will consist of even-aged, second-growth forests. Unmanaged, these stands will provide very poor deer habitat. Research is needed on silvicultural prescriptions capable of improving habitat quality of second-growth stands. Techniques for accomplishing the prescriptions and the effects need to be evaluated.

Appendix

Common Name	Scientific Name
Animals	
mule and black-tailed deer	*Odocoileus hemionus*
Sitka black-tailed deer	*Odocoileus hemionus sitkensis*
Columbian black-tailed deer	*Odocoileus hemionus columbianus*
gray wolf	*Canis lupus*
Plants	
Alaska yellow cedar	*Chamaecyparis nootkatensis*
alectoria	*Alectoria spp.*
beard lichen	*Usnea spp.*
bunchberry	*Cornus canadensis*
devilsclub	*Oplopanax horridum*
Douglas-fir	*Pseudotsuga menziesii*
fireweed	*Epilobium angustifolium*
five-leaved bramble	*Rubus pedatus*
lace flower	*Tiarella trifoliata*
fernleaf goldthread	*Coptis aspleniifolia*
blueberry	*Vaccinium spp.*
early blueberry	*Vaccinium ovalifolium*
red huckleberry	*Vaccinium parvifolium*
single delight	*Monesis uniflora*
Sitka spruce	*Picea sitchensis*
skunk cabbage	*Lysichiton americanum*
violet	*Viola spp.*
western hemlock	*Tsuga heterophylla*
western redcedar	*Thuja plicata*

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